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GIANT CELLS INDUCED BY NEMATODES OF THE HETERODERIDAE

J. G. Baldwin

INTRODUCTION: Among the plant parasitic nematodes, members of the Heteroderidae show the greatest morphological adaptations to parasitism. Adult females are sedentary obligate parasites. They must feed at a localized site without killing the host cells which supply their food. Plant cells which differentiate normally are not known to meet this requirement. Therefore, the nematode must induce and sustain a transformation of host tissues, so that the cells maintain homeostasis as their cytoplasm is withdrawn. Such modified cells were first described by Treub in 1887, and are generally called giant cells or syncytia, although other names such as nurse cells and lysigenoma have been suggested. These enlarged, multinucleate cells have been described in many host species and have been compared with other abnormal tissues such as cancerous cells and bacteria-induced crown galls. Among approximately 12 genera of Heteroderidae, host responses have been described for only a few, particularly Meloidogyne and Heterodera. Basic differences have been noted between giant cells induced by these 2 genera. Recently, considerable information has been gained concerning the morphology and physiology of these unusual cells.

CHARACTERISTICS COMMON TO GIANT CELLS: The morphology of giant cells has been examined with the light and electron microscope. As a giant cell develops, its cytoplasm becomes optically dense and granular, and the large central vacuole is replaced by increasingly more minute but numerous vacuoles. Endo (1971) noted that the cytoplasm closely resembles that of meristematic cells. It includes many organelles, and their abundance suggests a high level of metabolism.

Giant cells induced by Meloidogyne and Heterodera are multinucleate due to fusion of adjacent cells and/or repeated mitosis (of the nucleus) without cytokinesis. Nuclei may be irregularly-shaped and enlarged as much as 200 times that of normal nuclei. Such hypertrophy (enlargement) is indicative of especially active metabolism. Nuclei of a given syncytium may be of varying ploidy, and several investigators have suggested that some nuclei may fuse. Bird (1973) has observed that mitosis is synchronous in small syncytia, but in large syncytia there is a phase lag in mitosis throughout the cell.

Jones and several different associates (1972, 1975, 1976) have shown that morphology of the cell wall and plasmalemma (cell membrane) which follows its contours, is particularly important to understanding giant cells. These walls include numerous ingrowths which greatly increase the surface area of the plasmalemma. The increased surface area is most pronounced adjacent to vascular tissue, which is a potential site of nutrient influx into the giant cell. This adaptation for influx of solutes prompted Pate and Gunning (1972) to first consider nematode-induced syncytia as a type of transfer cell, with which the nematode acts as a "nutrient sink". Ingrowths occur to varying degrees on walls between giant cells. These walls become particularly thin and result in pit fields where plasmadesmata (connecting strands of cytoplasm between cells) are present. Therefore, exchange of materials among giant cells of a given cluster is likely. Jones and Dropkin (1976) did not find plasmadesmata between giant cells and adjacent nonsyncytial tissue.

The morphology of giant cells indicates a high level of metabolism, and this is confirmed by physiological investigations. Dropkin (1969) suggests that nematodes stimulate syncytia to increase synthesis of the products which they utilize; Jones and Northcote (1972b) note that increased metabolism is required for the synthesis of wall ingrowths, and to channel energy for concentration of nutrients from conducting vessels. Most enzymes assayed have greater activity in giant cells than in normal tissues. In addition, nucleic acids, amino acids, proteins, lipids, and possibly starch have been found to accumulate in certain giant cells. Jones and Dropkin (1975) have suggested that polysaccharides, which are synthesized throughout the life of the giant cell, may be the "main diet" of the nematode.

The precise mechanism by which nematodes induce formation of giant cells is not known, but Dropkin (1969) and Endo (1971) have reviewed investigations relevant to this problem. Many investigators have identified enzymes in nematodes which alter host tissues. In addition, the similarity between effects of nematodes and certain growth regulators is apparent, and auxin activity, as well as auxin inhibitors have been found in extracts of nematodes. Dropkin et al (1969) found that addition of the growth regulator, cytokinin, to the media, enabled large numbers of root-knot nematodes to induce giant cells and reproduce on a normally resistant cultivar of tomato. Exudates produced by the dorsal esophageal gland and released into the host through the stylet are thought to be particularly important to the development of giant cells. Bird (1974) notes that these exudates might include histone-like proteins which could interfere with normal regulation of the host genes and thus alter the cell's normal differentiating mechanism. In addition to stylet exudates, host tissues might also be affected by excretions from the nematodes' excretory pore, anus, or cuticle. Bird (1974) postulates that secretions from the amphid, which apparently include esterases in root-knot nematodes, could be involved in giant cell formation.

Contribution No. 178, Bureau of Nematology, Post Office Box 1269, Gainesville, Florida 32602

VARIATION AMONG GIANT CELLS INDUCED BY DIFFERENT GENERA: Differences may occur among giant cells with respect to site and mode of formation, morphology, and physiology. Meloidogyne and Heterodera induce giant cells primarily in the stele, whereas Ruehle (1962) found that giant cells of Meloidodera occurred in the cortex. Meloidogyne typically induces pericycle hyperplasia (proliferation of cells) and cortical hypertrophy, which results in galled roots, whereas, Heterodera is less likely to form galls. Giant cells induced by Heterodera form by dissolution of walls between cells and subsequent merging of protoplasts, but this process, if it occurs at all, is thought to be much more limited in giant cells induced by Meloidogyne. In the latter case, syncytia are derived primarily from repeated mitosis without cytokinesis. This difference in formation is reflected in mature giant cells. Those of Meloidogyne are discrete units, whereas those of Heterodera have many remnants of cell walls, and extensive gaps between giant cells of a given cluster. Jones and Northcote (1972) point out that giant cells of Meloidogyne generally form near the center of the root in differentiating xylem. These cells can expand equally in every direction and are usually clustered around the lip region of the parasite; therefore, the nematode can orient its head and feed, in turn, from different cells. On the other hand, giant cells of Heterodera are generally elongate, less clearly defined, and each cell is usually associated with a single nematode. Jones and Northcote (1972) note that syncytia of Heterodera form from tissues when the xylem is somewhat mature and lignified, and that this xylem limits expansion of the cell toward the cortex. One effect of this mode of development is that sieve elements on the cortical side of syncytia are crushed by developing cells associated with Heterodera, but not by Meloidogyne. Distribution of wall ingrowths in giant cells of Heterodera affirms that solutes are obtained from xylem, with which the elongate cells have considerable contact, but in giant cells associated with Meloidogyne solutes are secured from both xylem and phloem.

CONCLUSIONS: Giant cells induced by Meloidogyne and Heterodera have striking differences which could reflect a fundamental distinction between the genera. According to Wouts (1972) the spherical shape of the female is the only basic morphological character held in common between these genera. It follows that the shape of the female requires that it be sedentary, and that certain host cells be modified for sustained feeding at a localized site. Additional research may further confirm that the resemblance of giant cells of these genera is superficial, and could support Wouts (1972) view that Heterodera and Meloidogyne should be placed in separate families. Further work needs to be done to determine the nature of giant cells of other genera of Heteroderidae, and how they compare to those of Heterodera and Meloidogyne.

Knowledge of nematode-induced giant cells has greatly expanded in recent years. Yet integrating the available information into a complete "model" of the giant cell is not yet possible. According to Bird (1974) the chemicals responsible for syncytial formation and maintenance probably act in such minute quantities, that histochemical and bioassay techniques of sufficient sensitivity to characterize them have not yet been developed. Bird (1974) further states that the critical problems in understanding giant cells will probably be resolved by concerning ourselves with the biology of cell differentiation. Better understanding of host-parasite relationships, including giant cells, could point to new approaches for regulating these relationships to favor the host and to control the destructive pathogens of the Heteroderiae.

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